

Genetics of cyst nematode resistance in soybean PIs 467312 and 507354

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Summary

Soybean Cyst nematode (SCN) *Heterodera glycines* Ichinohe is the most serious pest of soybean [*Glycine max* (L.) Merr.] in the world and genetic resistance in soybean cultivars have been the most effective means of control. Nematode populations, however, are variable and have adapted to reproduce on resistant cultivars over time due mainly to the narrow genetic base of SCN resistance in *G. max*. The majority of the resistant cultivars trace to two soybean accessions. It is hoped that new sources of resistance might provide durable resistance. Soybean plant introductions PI 467312 and PI 507354, are unique because they provide resistance to several nematode populations, i.e. SCN HG types 0, 2.7, and 1.3.6.7 (corresponding to races 3, 5, and 14) and HG types 2.5.7, 0, and 2.7 (corresponding to races 1, 3, and 5), respectively. The genetic basis of SCN resistance in these PIs is not yet known. We have investigated the inheritance of resistance to SCN HG types 0, 2.7, and 1.3.6.7 (races 3, 5, and 14) in PI 467312 and the SCN resistance to SCN HG types 2.5.7 and 2.7 (races 1 and 5) in PI 507354. PI 467312 was crossed to 'Marcus', a susceptible cultivar to generate F₁ hybrids, 196 random F₂ individuals, and 196 F_{2:3} families (designated as Pop 467). PI 507354 and the cultivar Hutcheson, susceptible to all known SCN races, were crossed to generate F₁ hybrids, 225 random F₂ individuals and 225 F_{2:3} families (designated as Pop 507). The F_{2:3} families from each cross were evaluated for responses to the specific SCN HG types in the greenhouse. Chi-square (χ^2) analyses showed resistance from PI 467312 to HG types 2.7, and 1.3.6.7 (races 5 and 14) in Pop 467 were conditioned by one dominant and two recessive genes (*Rhg rhg rhg*) and resistance to HG type 0 (race 3) was controlled by three recessive genes (*rhg rhg rhg*). The 225 F_{2:3} progenies in Pop 507 showed a segregation of 2:223 (R:S) for response to both HG types 2.5.7 and 2.7 (corresponding to races 1 and 5). The Chi-square analysis showed SCN resistance from PI 507354 fit a one dominant and 3 recessive gene model (*Rhg rhg rhg rhg*). This information will be useful to soybean breeders who use these sources to develop SCN resistant cultivars. The complex inheritance patterns determined for the two PIs are similar to the three and four gene models for other SCN resistance sources known to date.

Introduction

Soybean, grown for its edible protein and oil, is a very important agronomic crop worldwide. Unfortunately soybean yields are reduced each year by nematodes and diseases. Soybean cyst nematode *Heterodera glycines* Ichinohe (SCN), first discovered in

Japan and then identified in USA in 1954 reduces yield more than any other soybean pest in the world (Doupnik, 1993; Wrather et al., 2001). Resistant cultivars have been an effective means of control. Populations of *H. glycines*, however, are extremely variable (Ross, 1962; Miller, 1969; Riggs and Schmitt, 1988; Arelli, et al., 1992b; Anand et al., 1994 & Niblack

et al., 2002) and have overcome resistance in cultivars making them less effective in reducing yield losses. Variation in SCN was originally described by designating populations as races following a similar scheme for fungi. Initially four races were described, and later 16 were designated based on reaction of the nematode to four soybean genotypes (Riggs and Schmitt., 1988). Still the 16 race scheme was inadequate in describing variability of SCN populations. A new classification scheme for more accurate identification of genetically diverse populations of *H. glycines* has been proposed (Niblack et al., 2002). In the new scheme, 'HG type' was proposed instead of 'race'; and seven soybean indicator lines (Peking, PI 88788, PI 90763, PI 437654, PI 209332, PI 89772 and PI 548316) are currently used in determining HG types.

Injury in soybean caused by SCN mobilized research efforts in the USA to breed resistant cultivars and to search for sources of resistance in the germplasm collection. Soybean breeders and nematologists have been evaluating the soybean germplasm collection for resistance sources (Ross and Brim, 1957; Epps and Hartwig, 1972; Anand and Gallo, 1984; Anand et al., 1988; Young, 1990, 1995) primarily to populations of HG types 0, 2.7 and 1.3.6.7 (races 3, 5, and 14). A total of 118 resistant PI lines were identified with resistance to one or more of these HG types (Arelli et al., 1992b). Arelli et al. (1997, 2000) also bioassayed the 118 accessions to SCN populations of HG types 2.5.7 and 1.2.5.7 (corresponding to races 1 and 2). Although more than 100 SCN resistance sources have been identified, the genetic base of host resistance is narrow (Shannon et al., 2004).

Many SCN resistant cultivars have been developed in the USA although nearly all have derived resistance genes from Peking to HG types 2.5.7, and 0 (races 1 and 3) and/or PI 88788 to HG types 0, and 1.3.6.7 (races 3 and 14). Because of a restricted genetic base, the pathogen has adapted and overcome resistance in soybean cultivars due to shifts to virulent HG types (Dong et al., 1997, Shannon et al., 2004). In the USA HG types 2.5.7, 1.2.5.7 and 2.7 (races 1, 2, and 5) have especially become more predominant in states growing soybeans (Niblack et al., 2003). Thus, it is important to breeders to identify novel resistance genes from other sources for incorporation into cultivars to provide resistance to predominant SCN HG types in soybean fields.

Soybean Plant Introductions PI 467312 and PI 507354 have shown resistance to several SCN HG types and have other desirable traits. PI 467312 is a Maturity Group II germplasm accession from China with

greenish brown seed coat. The seed has high protein content, valuable for food feed and industrial applications. Young, (1995) reported it was resistant to SCN HG types 0, 2.7 and 1.3.6.7 (races 3, 5, and 14). Arelli et al., (2000) reported it was also moderately resistant to HG types 2.5.7 and 1.2.5.7 or races 1 and 2. PI 507354 of maturity group I was introduced from Japan and has yellow seed coat. Young, (1995) reported it had resistance to HG types 2.5.7, 0, and 2.7 (races 1, 3 and 5). Arelli et al. (2000) also showed PI 507354 had resistant to HG type 2.5.7 and 1.2.5.7 (races 1 and 2). This PI line also has good agronomic characteristics such as resistance to lodging and shattering. The early maturity of both PI lines makes them an attractive source for development of SCN resistant cultivars in maturity groups II and earlier in which fewer SCN resistant cultivars are available (Shannon et al., 2004). Inheritance of SCN resistance in these two PIs, however, has not been studied. Therefore, the objectives of our study were to determine the inheritance of resistance to SCN populations of HG types 0, 2.7 and 1.3.6.7 (corresponding to races 3, 5, and 14, respectively) in PI 467312; and to HG types 1.2.5.7 and 2.7 (corresponding to races 2 and 5, respectively) in PI 507454.

Materials and methods

Plant materials

Two populations, referred to as Pop 467 and Pop 507, were developed. Pop 467 was generated by crossing PI 467312 with 'Marcus' (Cianzio et al., 1990). Pop 507 was developed by crossing PI 507354 with 'Hutcheson' (Buss et al., 1988). Both Marcus and Hutcheson are susceptible to all known SCN populations. Pop 467 was produced in Puerto Rico at the Iowa State University research site located at the Isabela Substation, Univ. of Puerto Rico at Isabela, Puerto Rico. The parents were crossed in the spring of 1999 and F₁ seeds were grown in the summer of 1999 to generate 196 F₂ seed. The F₂ generation was grown during the winter of 1999–2000 to produce 196 F_{2:3} families. Seeds of F_{2:3} progenies from each F₂ plant were used for SCN bioassays to populations of SCN HG types 0, 2.7 and 1.3.6.7 (corresponding to races 3, 5 and 14) in the greenhouse. Pop 507 was developed at the University of Missouri – Delta Center Portageville, MO in 2001. One F₁ seed was grown in Costa Rica during the winter of 2001–2002. F₂ seeds were planted at the Bradford farm, University of Missouri-Columbia, MO during the

summer of 2002. Seeds from 225 $F_{2:3}$ progenies were produced and used for greenhouse bioassays to determine resistance to populations of SCN HG types 2.5.7, and 2.7 (races 1 and 5).

SCN bioassay and data analysis

Methods for the SCN bioassay performed in the greenhouse to determine SCN reaction of lines in Pops 467 and 507 to the various HG types followed established protocols by Arelli et al. (2000). Differentials or indicator lines included Pickett, Peking, PI 437654, PI 88788, and PI 90763. Hutcheson, susceptible to all known HG types, was the control. Female index (FI) was used to differentiate resistant and susceptible individuals based on the standard classification system of inoculating with a specific number of SCN larvae and counting the number of white female cysts on roots (Golden et al., 1970; Riggs and Schmitt., 1988; Schmitt & Shannon, 1992; Niblack et al., 2002). The female index was calculated as a percent as follows:

$$\text{FI (\%)} = \frac{\text{Mean number of females in a given subfamily}}{\text{Mean number of females on Hutcheson}} \times 100$$

A female index (FI) of $\leq 10\%$ was considered a resistant (R) reaction whereas a female index (FI) $> 10\%$ is defined as a susceptible (S) reaction. SCN reaction was based on white female development on five plants from each $F_{2:3}$ family in each of two replications. $F_{2:3}$ lines were classified into two categories resistant and susceptible. A frequency distribution was determined for reaction of lines within Pop 467 and Pop 507 to each HG type. The Chi-square (χ^2) test using the Yates correction analysis to adjust for small population size was used to test the goodness of fit for the gene models we proposed. In this study, each F_3 line used in different HG type or race bioassays was derived from a given F_2 individual. Hence, a single correlation coefficient analysis was used to study the relationship of resistant genes to different SCN HG types in Pop 467 and Pop 507.

Results and discussion

All HG types (SCN races) used in this study were confirmed according to reaction on the standard differentials and control (Hutcheson). Parents and differentials

Table 1. Mean female index and range (\pm) of $F_{2:3}$ lines each from Pop 467 and Pop 507, parents and indicator lines to SCN HG types (races)

Lines	HG type 2.5.7 race 1	HG type 0 race 3	HG type 2.7 race 5	HG type 1.3.6.7 race 14
PI 467312		5.6 \pm 3.2	0.8 \pm 1.7	7.8 \pm 5.4
Marcus		133.0 \pm 21.0	109.2 \pm 40.1	127.0 \pm 30.5
Pop 467		56.0 \pm 30.8	47.5 \pm 25.2	41.5 \pm 27.3
Hutcheson		100.0 \pm 37.2	100.0 \pm 34	100.0 \pm 21.0
Pickett		0.4 \pm 1.1	100.2 \pm 29.5	113.1 \pm 6.2
Peking		0.6 \pm 2.1	3.3 \pm 9.8	16.0 \pm 5.1
PI 88788		1.8 \pm 3.9	33.0 \pm 23.0	5.1 \pm 0.1
PI 90763		0.1 \pm 0.05	0.0	
PI 507354	2.1 \pm 1.9		5.7 \pm 6.4	
Hutcheson	100.0 \pm 49.9		100.0 \pm 37.8	
Pop 507	69.7 \pm 30.4		79.6 \pm 39.7	
Peking	0.5 \pm 0.6		4.7 \pm 3.2	
PI 90763	0.25 \pm 0.1		0.001	
PI 437654	0.5 \pm 0.8		0.001	
Pickett	0.75 \pm 1.0		48.1 \pm 15.1	
PI 88788	20.1 \pm 10.6		32.0 \pm 6.7	

included in all inoculations in this study exhibited reactions to the populations of HG types (races) consistent with protocols established by Riggs and Schmitt, (1988), Schmitt and Shannon, (1992), and Niblack et al., (2002). Significant variation was observed in the responses of $F_{2:3}$ families, parents and differentials, and also between replications for all SCN HG types (races) tested (Table 1), suggesting that the reactions of individual plants to SCN HG types are affected significantly by environment. Data from the SCN bioassays indicated that the responses to SCN HG types 0, 2.7 and 1.3.6.7 (corresponding to races 3, 5 and 14) in Pop 467 and responses to SCN HG types 2.5.7 and 2.7 (races 1 and 5) in Pop 507 were normally or near normally distributed, respectively (Figs. 1 and 2). Therefore, the experimental design and data collection were proper for further genetic analysis.

Inheritance of Resistance genes in PI 467312 and PI 507354

Segregation ratios and chi-square analyses for the 196 families in Pop 467 tested against SCN HG types 0, 2.7 and 1.3.6.7 (races 3, 5 and 14) are presented in Table 2. There were 193 susceptible and 3 resistant $F_{2:3}$ families observed to HG type 0 (Race 3). Reaction of Pop 467 to HG type 2.7 (Race 5) showed 189 susceptible and 7 resistant $F_{2:3}$ families; and reaction to HG type 1.3.6.7 (race 14) 188 susceptible and 8 resistant $F_{2:3}$ families

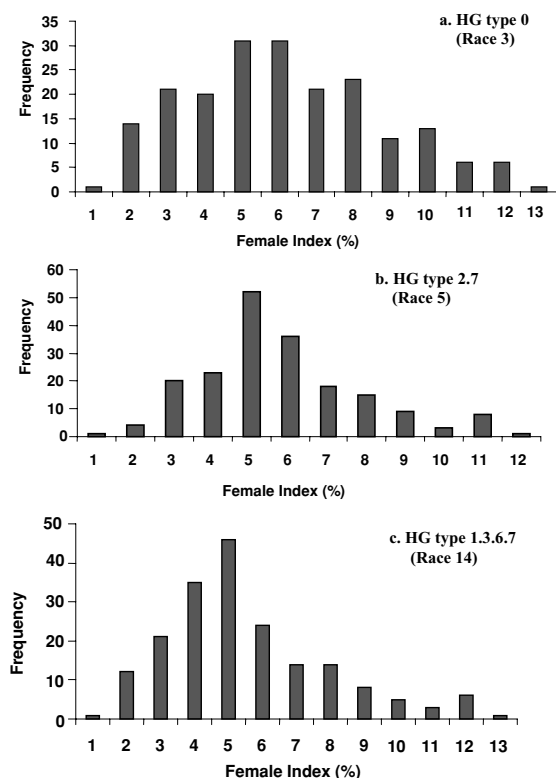


Figure 1. Frequency distribution for female index (FI) to SCN HG types 0, 2.7, and 1.3.6.7 (Races 3, 5, and 14) in Pop 467.

were observed, respectively. Chi-square analyses show that segregation ratios of susceptible and resistant families for SCN resistance in PI 467312 fit a three recessive gene (*rhg rhg rhg*) model for HG type 0 (race 3) with the p value for $\chi^2 > .95$ (Table 2). A one dominant and two recessive gene model (*Rhg rhg rhg*) was a good fit for reaction to both HG types 2.7 (Race 5) and HG type 1.3.6.7 (Race 14) with a p value for $\chi^2 > .50$ and $> .95$, respectively for each SCN population (Table 2).

In Pop 507, the 225 $F_{2:3}$ progenies showed a segregation of 2 resistant (R) and 223 susceptible (S) in response to both SCN populations and fit the genetic ratio of 3(R):253(S) (Table 3). Considering the small population size we studied, this is a good fit ($p = 0.95$) for one dominant and three recessive (*Rhg rhg rhg rhg*) gene model conditioning resistance to both HG types 2.5.7 and 2.7 (races 1 and 5) in PI 507354.

The genetic data in PI 467312 and PI 507354 showing resistance involving three or four genes are consistent with previous studies that have shown inheritance of resistance to SCN is a complex trait. Three and four gene models have been proposed for SCN resistance in

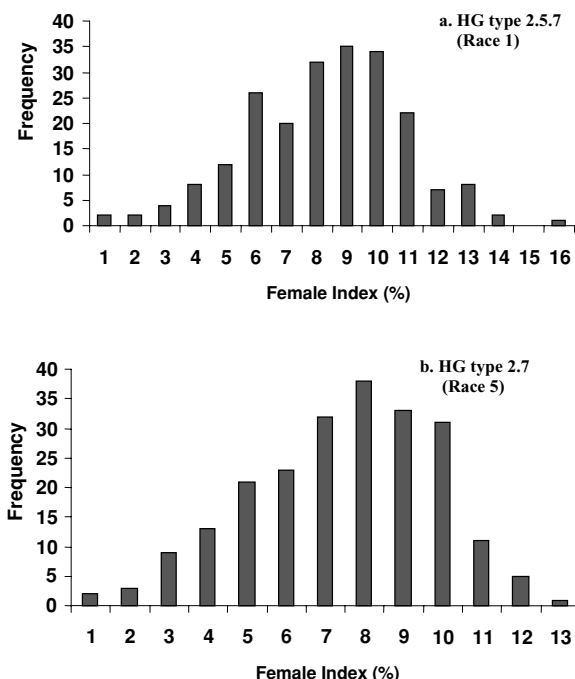


Figure 2. -Frequency distribution for female index (FI) to SCN HG types 2.5.7 and 2.7 (Races 1 and 5) in Pop 507.

studies with other resistance sources to HG types 2.5.7, 0, 2.7 and 1.3.6.7 (corresponding to races 1, 3, 5 and 14, respectively). Caldwell et al. (1960) reported the inheritance of soybean resistance to SCN and proposed three recessive genes (*rhg1*, *rhg2*, *rhg3*) were involved in resistance to SCN in the resistance source Peking. Later, a dominant gene (*Rhg4*) was additionally reported in Peking by Matson and Williams (1965). Inheritance of resistance to SCN HG type 1.3.6.7 (race 14) in PI 88788 was proposed to be conditioned by one dominant and two recessive genes (Thomas et al., 1975). Arelli et al. (1992a, 1994) identified an additional dominant gene *Rhg5* in PI 88788. In PI 438489B three genes (*rhg*, *rhg*, *rhg*) for HG type 1.3.6.7 (race 14); three genes (*Rhg*, *Rhg*, *rhg*) for HG type 2.7 (race 5); four genes (*Rhg*, *rhg*, *rhg*, *rhg*) for HG type 1.2.5.7 (race 2) and three genes (*Rhg*, *Rhg*, *rhg*) to HG type 2.5.7 (race 1) were necessary to confer high resistance to these four SCN populations (Yue et al., 2000).

Previous studies showed that some PIs had genes in common for SCN races. For example, Peking, PI 88788, PI 437654 and PI 90763 were reported to have at least one major QTL (Quantitative Trait Loci) in the same region on linkage group (LG) G for race 3 resistance. Several reports (Mahalingam and

Table 2. Chi square analysis of F_{2:3} lines in Pop 467 to SCN HG types 0, 2.7, and 1.3.6.7 (races 3, 5 and 14).

Races	Total	Number of plants Observed ratio R:S*	Expected ratio R:S*	Hypothesized resistance genes	Expected genetic ratios	χ^2	P-value
Race 3	196	3:193	3.1:192.9	<i>rhg rhg rhg</i>	1: 63	0.05	>0.90
Race 5	196	7:189	9.2:186.8	<i>Rhg rhg rhg</i>	3: 63	0.33	>0.50
Race 14	196	8:188	9.2:186.8	<i>Rhg rhg rhg</i>	3: 63	0.05	>0.90

* R = Resistant; S = Susceptible

Table 3. Chi square analysis of F_{2:3} lines in Pop 507 to SCN HG types 2.5.7 and 2.7 (races 1 and 5).

Races	Total	Number of plants Observed ratio R:S*	Expected ratio R:S*	Hypothesized resistance genes	Expected genetic ratios	χ^2	P-value
Race 1	225	2:223	2.6:222.4	<i>rhg rhg rhg</i>	3:253	0.0038	>0.95
Race 1	225	2:223	2.6:222.4	<i>rhg rhg rhg</i>	3:253	0.0038	>0.95

* R = Resistant; S = Susceptible

Skorupska, 1995; Arelli et al., 1992; Concibido et al., 1997; Webb et al., 1995; Lorenzen et al., 1995; and Concibido et al., 2004) show some of these PIs share QTLs in common for resistance to both HG types 0, and 1.3.6.7 (races 3 and 14). PI 437654, PI 90763 and PI 438489B (Myers et al., 1989; Yue et al., 2001b) were additionally indicated to have some genes in common for resistance to HG types 2.7 and 1.3.6.7 (races 5 and 14).

Fingerprinting data (P. Arelli, personal communication) show that PI 467312 and PI 507354 were distantly related to PI 88788, Peking, PI 90763, PI 209332, and PI 437654 which have been used in developing SCN resistant cultivars or germplasm lines. It was hypothesized that they would have a high probability of offering novel SCN resistance genes different from genes previously reported. The allelic relationship of resistance between PI 507354 and PI 467312 and other reported resistant sources are not currently well understood.

Relationships of resistance to different SCN races

From the greenhouse bioassay, we observed a few F_{2:3} families in both populations that possessed high resistance to multiple SCN HG types. In Pop 467, we observed that two F_{2:3} families had complete resistance to HG types 0, 2.7 and 1.3.6.7 (races 3, 5 and 14) and one family was resistant to HG types 0 and 2.7 (races 3 and 5). In Pop 507, two families were highly resistant to both HG types 2.5.7 and 2.7 (races 1 and 5). The

reactions to different SCN HG types for the same F_{2:3} families were evaluated through correlation analysis in both populations. The results (Table 4) show that reaction to different SCN races are highly correlated at the 1% level of significance. In the evaluation of the soybean germplasm collection for reaction to various HG types, some soybean germplasm lines were identified to be resistant to multiple SCN HG types (Anand et al., 1989; Young, 1994, 1995; Arelli et al., 2000). Concibido (1996) declared that a QTL on LG G conditioned SCN resistance to HG types 2.5.7, 0 and 1.7 (races 1, 3 and 6). Yue et al. (2000, 2001a, 2001b) reported that the phenotypic responses to several SCN populations are highly correlated and several marker intervals on LG G, B1, D1 and E were associated with multiple SCN races, respectively. Other studies (B. Guo, personal communication) also indicated that some common molecular markers are closely linked and are responsible for multiple SCN HG type resistance. This in-

Table 4. Correlation coefficients of reaction of F_{2:3} lines to the different SCN HG types (races) in Pop 467 and Pop 507

	HG type 2.5.7 (race 1)	HG type 0 (race 3)	HG type 2.7 (race 5)	HG type 1.3.6.7 (race 14)
Pop 467 (196) ^a				
Race 3			0.33**	0.41**
Race 5				0.37**
Pop 507 (225) ^a				
Race 1			0.31**	

^athe number of F_{2:3} families

dicates that some SCN resistance genes might be common or could be tightly linked in conditioning the reactions to different SCN HG types (races). Genetics of SCN resistance in PI 467312 and PI 507354 like other resistance sources is complex, but could contain different genes for resistance. Molecular mapping of SCN resistance QTL in these two PIs are underway and will facilitate a better understanding of resistance genes and their relationship to genes from other SCN resistance sources.

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